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Suppression of salient stimuli inside the focus of attention

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Abstract

We investigated how attention is distributed when one of two attended stimuli stands out from the visual context. Participants judged whether the line orientations within two geometric shapes at two predictable locations were same or different, which induced a wide focus of attention around the two locations. One of the geometric shapes surrounding the lines could be a salient color or shape singleton but was irrelevant for the task. In Experiment 1, the salient and non-salient items were both placed on the horizontal midline. Electrophysiological recordings at posterior electrode locations PO7/8 revealed a positivity between 200 and 300 ms contralateral to the singleton, consistent with the occurrence of the P_D. The P_D is thought to reflect attentional suppression. In Experiment 2, one attended item was placed on the vertical meridian and the other one on a lateral position. Lateral line targets triggered robust N2pc components when there was no singleton present, reflecting attentional selection. However, this N2pc to lateralized line targets was abolished when a singleton was presented at the same lateral position, and conversely, was increased when a singleton was presented on the vertical position. This suggests that salient elements inside the focus of attention are suppressed and attention is enhanced at the other location. It can be concluded that salient elements inside the focus of attention do not capture attention, as bottom-up control of attention would propose, but that salient elements are suppressed, possibly to assure unbiased processing of equally relevant stimuli.

Keywords

visual search, attentional capture, distractor suppression, focus of attention, divided attention, P_D, N2pc, Ppc

Introduction

In the present study, we asked how attention is distributed between a salient and a non-salient stimulus when both must be attended. We used a same-different task that provided no incentive to allocate more attention to one stimulus than to the other because the two attended stimuli had to be compared. The response-relevant target stimuli were horizontal or vertical lines at two fixed locations. The lines were surrounded by task-irrelevant geometric shapes (circles and squares; see Figure 1). On half of all trials, the shapes at the attended locations were identical. However, on the remaining trials, the shape at one of the response-relevant location was salient with respect to its color or shape. In previous studies requiring attention to more than one object, the stimuli were perceptually similar, probably to facilitate the parallel allocation of attention. It was observed that attention could be equally distributed among a number of stimuli (Wendt, Kähler, Luna-Rodriguez, & Jacobsen, 2017), but it is unclear whether the focus of attention was split (Kramer & Hahn, 1995; Müller, Malinowski, Gruber, & Hillyard, 2003), rapidly shifted (B. A. Eriksen & Eriksen, 1974; Posner, 1980), or expanded (C. W. Eriksen & St James, 1986; Heinze et al., 1994). For our present purposes, we only retain the basic notion that the response-relevant items were inside the focus of attention, regardless of whether the focus was split, shifted, or expanded.

Our stimuli resembled those used in the additional singleton paradigm (Theeuwes, 1991), which has provided only inconclusive evidence for attention either to be drawn towards or to be suppressed at the location of a salient stimulus. In the most common variant of the additional singleton paradigm, observers search for a shape singleton (e.g., a unique shape) and on some trials, a salient-but-irrelevant color singleton (e.g., a unique color) is shown. There is large consensus that reaction times increase when a color distractor is present, but there is no consensus on why this is the case. Bottom-up theories of attentional control hold that attention is involuntarily drawn to the most salient element even when it is task irrelevant, which causes a delay in search for the target (reviews in Awh, Belopolsky, & Theeuwes, 2012; Carmel & Lamy, 2015; Itti & Koch, 2001). On the other hand, there are studies suggesting that salient-but-irrelevant stimuli are suppressed (reviewed in Gaspelin & Luck, 2018). For instance, letters at the location of the distractors are reported less frequently (Gaspelin, Leonard, & Luck, 2015) and goal-directed movements stray less frequently to the distractor location (Gaspelin, Leonard, & Luck, 2017).

Further evidence for the different accounts comes from experiments employing electrophysiological (EEG) measures. Two event-related potential (ERP) components, the N2pc and P_D, were used to provide direct evidence for both attentional capture and attentional suppression in the additional singleton paradigm. The N2pc and P_D components occur in the same time interval from about 180 to 300 ms after stimulus onset and are localized at the same lateral posterior electrode sites (PO7/PO8) over extrastriate visual cortex. The N2pc is a contralateral negativity and is considered a marker of attentional object selection (Eimer, 1996; Luck & Hillyard, 1994) (Footnote 1). Because the N2pc was found to be triggered in response to lateral distractors in the additional singleton paradigm (Barras & Kerzel, 2017; Burra & Kerzel, 2013; Hickey, McDonald, & Theeuwes, 2006; Kiss, Grubert, Petersen, & Eimer, 2012), it was concluded that attention was captured by the salient stimulus. In contrast, the P_D is a contralateral positivity that is considered evidence for attentional suppression (Hickey, Di Lollo, & McDonald, 2009) and has also been observed to lateral distractors in the additional singleton paradigm (e.g., Barras & Kerzel, 2017; Burra & Kerzel, 2013; Feldmann-Wüstefeld & Schubö, 2013; Gaspar & McDonald, 2014; Hilimire, Hickey, & Corballis, 2012; McDonald, Green, Jannati, & Di Lollo, 2013; Sawaki, Geng, & Luck, 2012; Sawaki & Luck, 2010).

We defer discussion of the conditions promoting electrophysiological evidence of capture and suppression to the General Discussion, because for our present purposes, it is sufficient to retain that salient-but-irrelevant stimuli may result in either capture or suppression in visual search. The question of the present study is whether one or the other would occur when attention is distributed across two locations in a task that does not involve search. Previous evidence for attentional capture and suppression of distractors mostly involved search for a shape-defined target whose position varied unpredictably from trial to trial. In contrast, we asked participants to compare stimuli at two fixed and therefore predictable locations.

Experiment 1

In Experiment 1, observers were required to compare the line orientations inside two geometric shapes placed on the horizontal midline (left/right of fixation; see Figure 1). On half of all trials, the geometric shape at one of the two attended locations was visually salient because its color or shape differed from the remaining elements. We recorded EEG and measured the lateralized activity with respect to this featural discontinuity. Crucially, the

lateralized activity to the two response-relevant lines on either side of fixation should cancel each other out. Both lines were equally relevant for the comparison task, had to be attended and should therefore both trigger contralateral negativities (N2pc components) of equal size (Footnote 2). As a matter of fact, it is not possible to calculate an N2pc or P_D in the singleton-absent condition because there is no unique lateralized stimulus. Therefore, we expect a balanced voltage distribution at electrode sites PO7/8 with respect to the response-relevant features presented in the display. In contrast, the salient stimulus surrounding one of the two lateral lines may tip the scales: Attentional capture by the salient stimulus should be reflected in a contralateral negativity (N2pc component), whereas suppression should produce a contralateral positivity (P_D component). Our approach relies on the rationale that the N2pc and P_D components sum up or cancel out across hemifields (see Gaspar & McDonald, 2014; Hickey et al., 2009). In particular, any lateralized activity in the event-related potential (positive or negative) is thought to result from processing of the featural discontinuity and not from processing of the inconspicuous bilateral line elements whose activity will be nullified across hemifields. Therefore, a contralateral negativity (N2pc) with respect to the singleton location, elicited in the N2 time window, would suggest that the singleton was attentionally selected, while a contralateral positivity (P_D) in that time window would reflect attentional suppression of the singleton. Alternatively, there might be no lateralized activity at all during the N2 time period, which would indicate that attention was distributed equally across the two target locations, despite the fact that one of them contained a salient featural discontinuity and the other did not.

These predictions also rely on the assumption that the response-irrelevant shapes surrounding the target lines are attentionally processed. That is, a single focus of attention is either shifted rapidly between the two relevant target locations or is expanded to include both target locations for parallel processing (Eimer & Grubert, 2014; Grubert & Eimer, 2016a). For instance, the attentional focus may take on the shape of an ellipse including the two lateral positions and (at least part of) the surrounding shapes (e.g., Pan & Eriksen, 1993). Because stimulus presentation time was unlimited, and the task was easy, one of those scenarios is likely to occur (Jans, Peters, & De Weerd, 2010).

Further, in an exploratory fashion, we investigated whether there would be an early, salience-driven positivity in the N1 time range from about 140 to 190 ms, which is most often associated with the automatic processing of a contralateral feature discontinuity

(Barras & Kerzel, 2016; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicœur, 2012; Gokce, Geyer, Finke, Mueller, & Töllner, 2014; Jannati, Gaspar, & McDonald, 2013; Sawaki & Luck, 2010) even though there is some evidence for the implication of attention (Barras & Kerzel, 2017; Weaver, van Zoest, & Hickey, 2017). We refer to this component as Ppc (positive posterior contralateral, Fortier-Gauthier et al., 2012; Leblanc, Prime, & Jolicoeur, 2008). Finally, a contralateral positivity may also follow the N2pc (after about 300 ms) which has been associated with the termination of an attention shift or attentional suppression (Hilimire & Corballis, 2014; Hilimire, Mounts, Parks, & Corballis, 2011; Liesefeld, Liesefeld, Töllner, & Müller, 2017; Sawaki & Luck, 2013). While positive deflections both before and after the N2 time range have been labelled P_D, we reserve that label for a contralateral positivity in the N2 time range, indicating attentional suppression as opposed to attentional selection in the critical time window.

Methods

Participants. Twenty first-year psychology students from the University of Geneva participated for class credits (mean age ± standard deviation = 21.95 ± 8.86 years, 3 male), but only seventeen were retained in the final sample (20.12 ± 1.65 years, 3 male). The study was approved by the ethics committee of the Faculty of Psychology and Educational Sciences and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was given before the experiment. Sample size was determined based on Experiment 2 in Barras and Kerzel (2016) where we observed a significant P_D with 12 participants. Because the P_D had a mean amplitude of 0.61 µV with a SD of 0.61, a sample size of 8 would be sufficient to reach a power of 0.8 with a Type 1 error rate of 5%.

Apparatus and stimuli. Stimuli were displayed on a 21-inch CRT monitor with a refresh rate of 85 Hz and a pixel resolution of 1280 × 1024 (horizontal x vertical), viewed at approximately 80 cm. The background was black, and the stimuli were either red or green (CIE coordinates x = 0.628, y = 0.338 for red, and x = 0.294, y = 0.605 for green). All stimuli had the same physical luminance of 16.5 cd/m^2. A gray fixation cross was presented in the center of the screen. The stimulus array was presented on a virtual circle with an eccentricity of 3.5° of visual angle. The search array consisted of eight equally spaced items, with two items on the horizontal midline. The outline shapes were circles (diameter 1.5°) and squares (side length 1.1°). Stroke width and size were slightly adjusted to give the same number of

colored pixels (720) for each shape. A vertical or horizontal gray line of 0.75° length was presented in the center of each shape. Stroke width was approximately 0.06° for all items.

Electrophysiological recording. An actiCHamp amplifier (Brain Products, Gilching, Germany) with active Ag/AgCl electrodes was used. Continuous EEG was sampled at 1000 Hz from 26 scalp electrodes and six additional electrodes placed at the outer canthi of each eye (bipolar HEOG), above and one below the right eye (VEOG), and on each earlobe (bipolar offline reference). Cz served as online reference and AFz as ground. Impedances were kept below 25 kΩ.

Offline, the data were analyzed using ERPLab (Lopez-Calderon & Luck, 2014). Raw EEG was re-referenced to the average of both earlobes and band-pass filtered between 0.1 and 30 Hz. In singleton-present trials, EEG was segmented into 500 ms epochs extending from 100 ms before to 400 ms after stimulus onset. The first 100 ms served as ERP baseline. Trials contaminated with behavioral errors, RTs slower than 2 secs, blinks and vertical eye movements (difference in VEOG channels exceeding ± 50 μV), horizontal eye movements (steps in HEOG channel exceeding ± 16 μV), and muscular artifacts (any electrode exceeding ± 80 μV) were excluded from analysis. On the remaining trials, separate averages were computed for color or shape singletons in the left and right hemifield, respectively.

Exclusion of datasets. One dataset was excluded because the average HEOG trace for left and right singletons was partially outside +/- 3 μV. Two further datasets were discarded because more than 40% of the data were lost due to artefacts or behavioral errors. With this rejection criterion, we assured an average of 155 trials per condition of interest (ranging from 101-181 trials across participants). Overall, 17 datasets were retained for the final analysis.

Procedure. Participants were asked to compare the line orientations of the stimuli on the left and right of fixation (i.e., at the 9 and 3 o'clock position) and respond "same" or "different" by pressing the arrow-left or arrow-right keys on a standard keyboard with their right hand. Key-to-response mapping was counterbalanced across participants and "same" and "different" responses were equiprobable. The response assignment was counterbalanced across participants. Participants were asked to maintain fixation on the central fixation cross, to ignore the colors and the shapes, and to respond as rapidly as possible while keeping the error rate below 10%. After blocks of 32 trials, the error rate was shown for 3 secs, allowing participants to take a short break. At the beginning of the

experiment, participants practiced the experimental task until they felt comfortable with it. Practice trials were not recorded, but participants completed at least 30 trials.

A trial started with the presentation of the fixation cross for a randomly selected duration between 0.5 and 1 sec. Then, the display appeared and stayed on the screen until a response was registered. Choice errors and late trials (RTs > 2 secs) were reported to the participant by visual feedback.

Outline colors and shapes were identical for all stimuli on a given trial except the singleton (when present). However, color (red or green) and shape (circle or square) varied independently and randomly from trial to trial. Red and green changed randomly to cancel out known asymmetries in color processing (Fortier-Gauthier, Dell'Acqua, & Jolicoeur, 2013; Pomerleau, Fortier-Gauthier, Corriveau, Dell'Acqua, & Jolicœur, 2014) and the random variation was introduced to maximize the effect of singletons on attentional processing (Kerzel & Barras, 2016). The experiment was separated into two blocked conditions of 386 trials. In the colour singleton condition, one of the stimuli at the two attended locations had a different color on 50% of the trials. In the shape singleton condition, one of the stimuli at the two attended locations had a different shape on 50% of the trials. Block order was counterbalanced across participants. The singleton appeared equally likely on the left and right. The number of vertical and horizontal lines inside the geometric shapes was the same and their distribution was random.

Behavioral Results

Trials with RTs slower than the online criterion of 2 secs were excluded from analysis (0.2%). Subsequently, data were trimmed for each participant and condition by removing trials with RTs exceeding 2.5 times the standard deviation from the condition mean. This resulted in the exclusion of additional 2.5% of the trials for the behavioral analysis.

RTs. Mean individual RTs were entered into a repeated-measures 2 (singleton feature: color, shape) x 2 (singleton presence: present, absent) x 2 (response: same, different) ANOVA. Means are shown in the upper panels of Figure 2. Besides a number of main effects and interactions that are not reported for brevity, there was a three-way interaction, $F(1, 16) = 19.20$, $p < .001$, $\eta_p^2 = .546$, which we followed up by running two-way ANOVAs (singleton presence x response), separately for each singleton feature. For the color singleton (see upper left panel in Figure 2), there was only a main effect of response, $F(1, 16) = 36.58$, $p < .001$, $\eta_p^2 = .696$, showing that “same” responses were faster than “different”

responses (648 vs. 694 ms). Faster RTs for "same" than "different" responses have been reported in some (Pan & Eriksen, 1993; Wendt et al., 2017), but not all studies (Egeth, Jonides, & Wall, 1972). For the shape singleton (see upper right panel in Figure 2), there was a two-way interaction of singleton presence and response, $F(1, 16) = 51.92$, $p < .001$, $\eta_p^2 = .764$, which modulated the main effects of singleton presence $F(1, 16) = 27.78$, $p < .001$, $\eta_p^2 = .635$, and response, $F(1, 16) = 26.84$, $p < .001$, $\eta_p^2 = .627$. The two-way interaction showed that "same" responses were slower when a shape singleton was present compared to when it was absent (694 vs. 623 ms), $t(16) = 8.17$, $p < .001$, Cohen's $d = 1.98$, which was not the case for different responses, $p = .283$.

Choice errors. The same ANOVA as above was run on mean percentage of choice errors. Besides other effects, we confirmed a three-way interaction $F(1, 16) = 9.55$, $p = .007$, $\eta_p^2 = .374$, and ran two-way ANOVAs to follow up. The two-way ANOVA on trials from color blocks did not reveal any significant effects. Mean percentage of errors was 5.3%. The second two-way ANOVA on RTs from shape blocks revealed a significant two-way interaction, $F(1, 16) = 21.74$, $p < .001$, $\eta_p^2 = .576$, which modulated the main effect of singleton presence, $F(1, 16) = 21.74$, $p < .001$, $\eta_p^2 = .576$. More errors occurred with "same" responses when a shape singleton was present compared to when it was absent (12.1% vs. 2.8%), $t(16) = 5.67$, $p < .001$, Cohen's $d = 1.38$, whereas singleton presence did not affect "different" responses (6.2% vs. 5.2%), $p = .291$.

Electrophysiological Results

After rejecting trials with electrophysiological artefacts, behavioral errors or RTs longer than 2 secs, 80.7% of the singleton-present trials remained for analysis (i.e., 159 trials on average for color and 150 trials for shape singletons per participant). The ipsi- and contralateral potentials at electrodes PO7/8 and the respective difference waves (obtained by subtracting ipsi- from contralateral activity) are shown in Figure 3. Ppc and N2pc/P_D mean amplitudes were measured at lateral posterior electrode sites PO7/8 in 50 ms time windows centered on the peaks of the N1 (166 ms after stimulus onset) and N2 (269 ms for color, 273 ms for shape) components of the non-lateralized ERP, respectively. Solid contralateral positivities were elicited in response to task-irrelevant color and shape singletons during both the N1 and N2 time windows. To substantiate these observations, mean difference amplitudes (contra minus ipsilateral), measured in the respective N1 and N2 time windows, were subjected to a repeated-measures 2 (analysis interval: N1, N2) x 2 (singleton feature:

color, shape) ANOVA (Footnote 3). Only the interaction approached significance, $F(1, 12) = 3.55$, $p = .078$, $\eta_p^2 = .182$, suggesting that the positivity tended to be larger with shape than with color singletons in the N2 interval (0.77 vs 0.41 μV), $t(16) = 1.91$, $p = .075$, Cohen's $d = 0.43$, whereas there was no difference in the N1 interval (0.34 vs. 0.48 μV), $p = .494$. One-sample t-tests against zero revealed that the positivity in the N1 interval was significant for color (0.48 μV), $t(16) = 2.90$, $p = .010$, Cohen's $d = 0.7$, and shape singletons (0.34 μV), $t(16) = 3.87$, $p = .001$, Cohen's $d = .94$. In other words, color and shape singletons triggered reliable Ppc components. Similarly, the positivity in the N2 interval was significant for color (0.41 μV), $t(16) = 2.80$, $p = .013$, Cohen's $d = 0.68$, and shape singletons (0.77 μV), $t(12) = 4.09$, $p = .001$, Cohen's $d = 0.99$, showing that the P_D component occurred to both types of singletons.

Discussion

We observed a contralateral positivity to salient feature discontinuities when two locations on opposite sides of fixation were attended. Note that only the line orientations were necessary to perform the task so that the color or shape singleton around the lines could have been entirely ignored. Critically, the P_D to color and shape singletons suggests that there was attentional suppression of the salient element inside the focus of attention, demonstrating that inhibitory selective mechanisms can be transiently deployed within the focus of attention. The P_D and the preceding Ppc were of equal magnitude for color and shape. The Ppc has often been reported for color discontinuities (Barras & Kerzel, 2016; Fortier-Gauthier et al., 2012; Gokce et al., 2014; Jannati et al., 2013), but only rarely for shape discontinuities (Barras & Kerzel, 2017). Consistent with this pattern, the Ppc to shape was very small in the present experiment and was not replicated in Experiment 2.

Behaviorally, we observed that “same” responses were generally faster except when a shape singleton was present. In this case, RTs tended to be longer, which resulted in a three-way interaction in the above ANOVA. Slower "same" responses with a shape singleton are reminiscent of a study by Keren, Ohara, and Skelton (1977) who reported that RTs on “same” trials in a letter-matching task were longer when a nonmatching distractor letter was present, despite the distractor location being irrelevant for the task. Perhaps, a shape singleton activated a “different” response because of the featural similarity between line

orientation and shape, resulting in interference with "same" responses. In contrast, a color singleton was sufficiently dissimilar from line orientation to avoid interference.

Further, it is unclear how to dissociate a P_D to the singleton from an N2pc to the non-singleton on the opposite side. The resulting voltage difference would be the same. Possibly, the color or shape singleton made it easier to filter out the line orientation from the immediately surrounding geometrical shape. Thus, filtering was more challenging at the opposite, non-singleton location, which may have provoked an N2pc. Feature overlap between the target and the surrounding non-targets is known to increase the amplitude of the N2pc (Hopf, Boelmans, Schoenfeld, Heinze, & Luck, 2002; but see Töllner, Zehetleitner, Gramann, & Müller, 2011). However, the filtering account predicts an asymmetry between shape and color singletons that is not observed in the electrophysiological data. Based on the feature similarity between shape and line orientation, which is substantiated by the pattern of RTs, one would predict that the N2pc to the non-singleton location was strong for shape, but absent or weak for color. What we observed, however, was that the voltage difference in the N2 interval was significant for color and only marginally larger for shape. Therefore, it seems unlikely that differences in filtering between the singleton and non-singleton locations account for the findings.

Importantly, there were no signs of behavioral interference from color singletons, which differs strongly from results in the additional singleton paradigm where search was disrupted by a salient color singleton (Theeuwes, 1991). The original interpretation of interference from a salient distractor was that attention was attracted to the location of the salient element, which incurred a cost because target and distractor location never coincided (reviewed in Lamy, Leber, & Egeth, 2012; Theeuwes, 2010). In contrast, the color singleton in the present study was always presented in one of the two attended locations. Therefore, the singletons never deviated attention away from the attended locations, which may explain why RTs were unaffected by the presence of a color discontinuity. In other words, the singletons in the present experiments did not act as distractors in the same way as color singletons in visual search tasks.

Experiment 2

In Experiment 1, the two response-relevant locations were both on the horizontal midline. Because both stimuli were lateralized and presented simultaneously, a positivity to the salient element on one side can theoretically not be disentangled from a larger N2pc to

the non-salient element on the other side. Both attentional suppression of the salient singleton and attentional enhancement of the non-singleton stimulus on the opposite side would result in a net positivity contralateral to the salient singleton. Therefore, our interpretation that observers suppressed the salient element needs further support. To isolate the electrophysiological response to each of the two attended elements, we presented one of them on the vertical meridian. Because the N2pc (and for this matter also the P_D) is calculated by comparing contra- and ipsilateral activity, a stimulus on the vertical meridian cannot trigger a lateralized ERP component, such as the N2pc (Woodman & Luck, 2003) or the P_D.

In Experiment 2, observers compared one stimulus on a lateral position to one stimulus on a central position (Figure 1, bottom panels). Target positions were still predictable, but the lateral stimulus position was changed after blocks of trials, while the vertical position was fixed for each participant. We measured ERPs in response to the lateralized task-relevant stimulus when it was surrounded by a singleton (lateral singleton), when the singleton was presented on the vertical meridian (central singleton), and when the singleton was absent. The singleton-absent condition in Experiment 2 served as a baseline for the size of the N2pc to lateralized line targets. If the salient singleton inside the focus of attention was suppressed, we should find an attenuated (or even completely abolished) N2pc in the lateral singleton condition as compared to the singleton-absent condition. This is because the N2pc to the lateral response-relevant line would combine with a P_D to the salient-but-irrelevant feature discontinuity presented at the same location (see Gaspar & McDonald, 2014; Hickey et al., 2009). If the presence of a feature discontinuity enhanced attention at the alternative target location inside the focus of attention, the N2pc to lateralized targets should be increased in central singleton as compared to singleton-absent trials. Note that the lateral stimulus in central singleton and singleton-absent conditions was equally inconspicuous and that processing of the central singleton per se was not reflected in the lateralized ERPs.

Methods

The methods were as in Experiment 1 with the following exceptions. Participants compared the line orientations of a central (i.e., 12 or 6 o'clock position) and a lateral (i.e., 9 or 3 o'clock position) stimulus. The position of the central element was fixed for each participant but counterbalanced across participants. The attended lateral position was

changed after half of the experiment. The feature discontinuity (color, shape) changed midway through a block of trials with the same lateral position. The initial lateral position and the initial singleton attribute were counterbalanced across participants. Four blocks with 288 trials were run for a total of 1152 trials. The first and third block (where the attended lateral position changed) was preceded by about 30 practice trials. Thirteen students participated (20 ± 1.83 years, 2 male), but one dataset was excluded because more than 40% of all trials were removed during artefact rejection, leaving 12 datasets in the final sample (19.83 ± 1.8 years, 2 male).

Behavioral Results

Trials with RTs not meeting the online criterion of 2 secs (1%) and outliers (2.6%) were excluded from analysis.

RTs. Mean individual RTs were entered into a repeated-measures 2 (singleton feature: color, shape) x 2 (singleton presence: present, absent) x 2 (response: same, different) ANOVA. Inspection of the means in the lower panels of Figure 2 shows that the results of Experiment 2 mirror those of Experiment 1. Besides other effects, there was a three-way interaction, $F(1, 11) = 32.15$, $p < .001$, $\eta_p^2 = .745$, that we followed up by running two-way ANOVAs (singleton presence x response) for each feature discontinuity (color, shape). For the color singleton (see lower left panel in Figure 2), there was only a main effect of response, $F(1, 11) = 15.77$, $p < .001$, $\eta_p^2 = .589$, showing that "same" responses were faster than "different" responses (729 vs. 802 ms). For the shape singleton (see lower right panel in Figure 2), there was a two-way interaction of singleton presence and response, $F(1, 11) = 18.34$, $p < .001$, $\eta_p^2 = .625$, that modulated the main effect of response, $F(1, 11) = 11.82$, $p = .006$, $\eta_p^2 = .518$, and the marginal effect of singleton presence, $F(1, 12) = 3.52$, $p = .087$, $\eta_p^2 = .242$. The two-way interaction showed that RTs on "same" trials were slower when a shape singleton was present than when it was absent (758 vs. 714 ms), $t(11) = 5.06$, $p < .001$, Cohen's $d = 1.46$. In contrast, RTs on "different" trials tended to be faster when a shape singleton was present (783 vs. 805 ms), $t(11) = 2.02$, $p = .069$, Cohen's $d = 0.58$.

Choice errors. The same ANOVA as above was run on mean percentage of choice errors. Besides other effects, we confirmed a three-way interaction, $F(1, 11) = 8.54$, $p = .014$, $\eta_p^2 = .437$, and ran two-way ANOVAs to follow up. The two-way ANOVA on trials from color blocks did not reveal any significant effects, ps > .211. The mean percentage of errors was 7.2%. The second two-way ANOVA on RTs from shape blocks revealed a significant two-way

interaction, $F(1, 11) = 9.94$, $p = .009$, $\eta_p^2 = .475$, that modulated the main effect of singleton presence, $F(1, 11) = 17.04$, $p = .002$, $\eta_p^2 = .608$. For "same" responses, more errors occurred on singleton-present than on singleton-absent trials (13.8% vs. 5.5%), $t(11) = 4.86$, $p = .001$, Cohen's $d = 1.4$, whereas singleton presence had no effect on "different" responses, $p = .32$.

Electrophysiological Results

After exclusion of error trials, late trials, and trials containing artefacts, EEG was averaged separately for lateral singleton, central singleton, and singleton-absent trials. ERPs were locked to the lateral target position (left or right side, respectively) in all three conditions. As for Experiment 1, Ppc and N2pc mean amplitudes were measured at PO7/8 in the 50 ms time windows centered on the peaks of the N1 (169 ms post-stimulus) and N2 (263 ms post-stimulus) components of the non-lateralized event-related potential, respectively. After trial rejection, 86.3% of the trials remained for analysis. The mean number of trials per participant for lateral singleton, central singleton and singleton-absent trials was 124, 127, and 249 trials for color and 120, 124, 250 trials for shape, respectively. Mean contra- and ipsilateral ERPs, as well as the respective difference waves, are shown in Figure 4.

N1-interval. We conducted a within-subjects 2 (singleton feature: color, shape) x 3 (singleton position: lateral, absent, central) ANOVA on mean difference amplitudes (contra minus ipsilateral) measured in the N1 time window (see Figure 4). The ANOVA showed a significant main effect of singleton position, $F(2, 22) = 10.44$, $p = .001$, $\eta_p^2 = 0.487$, and a significant two-way interaction of singleton feature and singleton position, $F(2, 22) = 8.09$, $p = .002$, $\eta_p^2 = 0.424$. Inspection of the difference waves in Figure 4 suggests that the interaction was driven by a positivity in the N1 interval with lateral color singletons (green line in lower left graph) that was absent in the remaining conditions. Paired-samples t-tests confirmed that the mean voltage difference to lateral color singletons (0.72 µV) was more positive than the voltage difference to lateral non-singleton targets when the color singleton was absent (-0.25 µV), $t(11) = 3.92$, $p = .002$, Cohen's $d = 1.13$, or when a central color singleton was shown (-0.18 µV), $t(11) = 4.02$, $p = .002$, Cohen's $d = 1.16$. A one-sample t-test against zero confirmed that the positivity to the lateral color singleton was significantly different from zero (0.72 µV), $t(11) = 2.57$, $p = .026$, Cohen's $d = 0.74$, showing that a Ppc had occurred. In contrast, the mean voltage difference to a lateral shape singleton did not differ from the remaining shape conditions, ps > .223.

N2-interval. The same ANOVA as above was conducted on N2pc mean difference amplitudes. There was an effect of singleton position, $F(2, 22) = 28.03$, $p < .001$, $\eta_p^2 = .718$, but no effect of singleton feature, $p = .292$, and no interaction, $p = .875$. Thus, the N2pc differences between color and shape as suggested by Figure 4 were not reliable and singleton feature was collapsed for the remaining analyses. One-sample t-tests against zero showed that a significant N2pc was triggered in response to lateral non-singleton targets in both the central singleton (-1.3 μV), $t(11) = 3.24$, $p = .008$, Cohen's $d = 1.27$, and the singleton-absent condition (-0.87 μV), $t(11) = 4.89$, $p < .001$, Cohen's $d = 1.3$. A paired-samples t-test revealed that the N2pc was increased in the central singleton as compared to the singleton-absent condition (difference of 0.42 μV), $t(11) = 3.24$, $p = .008$, Cohen's $d = 0.94$. This pattern of results is in line with the idea that the salient singleton enhanced attention at the other, non-salient, target location inside the focus of attention. As can be seen from Figure 4, a lateral singleton did not seem to trigger an N2pc, or any lateralized voltage difference. Consistently, a one-sample t-test against zero did not uncover a reliable difference (-0.08 μV), $p = .712$. A paired-samples t-test confirmed that the difference between lateral singleton and singleton-absent activity was reliable (difference of 0.79 μV), $t(11) = 4.89$, $p < .001$, Cohen's $d = 1.41$. The absence of any lateralized activity in the lateral singleton condition suggests that the salient singleton inside the focus of attention was suppressed, and that the N2pc to the response-relevant line was therefore nullified by the singleton's P_D.

N2+100ms. As can be seen best in the difference waves of Figure 4, the N2pc component in central singleton and singleton-absent trials extends in a sustained fashion up to 400 ms post-stimulus and beyond (not visible in Figure 4). Importantly, such a late negativity is also triggered in lateral singleton trials, where there is no initial difference in the N2 time window. This may suggest that observers initially suppressed the singleton on the lateral position (during the N2 time) but inspected its locations approximately 100 ms later (~360 ms post-stimulus; note that stimulus displays were presented until response). In such a scenario, attention may have initially settled on the non-salient element (central position) and only then shifted to the salient element (lateral position). Conversely, this idea would predict a decrease of the negativity after the N2pc-interval when the singleton was on the central position (i.e., the central salient position is attended after the lateral non-salient position). To confirm or disconfirm this idea, we ran a 2 (time interval: N2, N2+100ms) x 2

(singleton feature: color, shape) x 3 (singleton position: lateral singleton, singleton absent, central singleton) ANOVA. The 50 ms analysis time windows were centered at the non-lateralized N2 peak (263 ms post-stimulus) and at 363 ms for the N2+100ms component. The main effect of time interval, $F(1, 11) = 11.41$, $p = .006$, $\eta_p^2 = .509$, showed that the voltage difference became more negative 100 ms after the N2 interval (-0.75 vs. -1.32 μV). The main effect of singleton position, $F(2, 22) = 29.93$, $p < .001$, $\eta_p^2 = .731$, confirmed that the negativity was smallest to the lateral singleton and increased when the singleton was absent or appeared at a central position (-0.49, -1.12, and -1.49 μV, respectively). Together with a non-significant interaction of time interval and singleton position, $F(2, 22) = 2.48$, $p = .107$, $\eta_p^2 = .184$, this does not provide conclusive evidence for the idea that attentional suppression of salient stimuli was followed by an attention shift to the salient element.

Discussion

Our results demonstrate that inhibitory and excitatory selective mechanisms can be transiently deployed within the focus of attention. We disentangled suppression of the salient element from enhanced attention to the alternative location by asking observers to compare the line orientations of a central and a lateral stimulus. In half of all trials, a singleton was absent and in the other half, a singleton was presented on either a lateral or a central position. In all trials, however, a lateral stimulus was attended (containing one of the two target lines), which allowed us to measure the Ppc and N2pc components with respect to this lateral position. The singleton-absent condition provided a baseline condition where we assumed that attention was equally distributed between the two attended locations. Compared to baseline, we found a heavily attenuated N2pc to the lateral singleton, suggesting attentional suppression of salient stimuli in the focus of attention. Further, we found a larger N2pc to the lateral element with central singletons, suggesting that attention was biased away from the salient stimulus on the central position and toward the non-salient stimulus on the lateral position. Thus, salient stimuli inside the focus of attention cause both inhibitory (reduced N2pc to the salient stimulus) and excitatory (increased N2pc to the non-salient stimulus) selective mechanisms. While this account may refer to a difference in selection probability, it is also possible that the two stimuli are selected with equal probability, but that the specific mechanism reflected in the N2pc is activated more strongly when there is a salience signal from a singleton at one location.

Thus, we found evidence for both attentional suppression of salient stimuli and simultaneous enhancement of non-salient stimuli within the focus of attention. Further, we pursued the hypothesis that attention was initially allocated to the non-salient location before it was directed to the salient location. Shifts of attention can be accurately tracked with the N2pc component and were shown to take about 100 to 150 ms (Woodman & Luck, 1999) or less (Grubert & Eimer, 2016b). Contrary to this hypothesis of sequential allocation of attention, we only observed a general increase of the contralateral negativity from the N2 to a N2+100ms-interval in all three task conditions, which argues against the idea of a systematic shift of attention from the non-salient to the salient stimulus. Such a hypothesis would have predicted a decrease of the negativity from the N2 to the N2+100ms interval in the central singleton condition, and no change at all in the singleton absent condition.

Further, the results from the N2+100ms interval showed that the contralateral negativity extended beyond the typical time interval of the N2pc. Numerous studies have reported a contralateral negativity after the N2pc time range, starting at about 300 ms post-stimulus. This component has been labeled sustained posterior contralateral negativity (SPCN, Jolicœur, Brisson, & Robitaille, 2008) or contralateral delay activity (CDA, Vogel & Machizawa, 2004). A hallmark of the CDA is that its amplitude increases with the number of items retained in visual working memory. Because the number of task-relevant items for the line comparison was always two, the differences between lateral, central, and no singleton conditions that occurred 100 ms after the N2pc are unlikely to reflect differences in visual working memory. In addition, it is unlikely that our choice of stimuli accounts for the prolonged negativity because we used the same stimuli as in two previous studies (Barras & Kerzel, 2016, 2017) where the contralateral negativity did not extend beyond the N2pc range. The most likely reason for the extended N2 negativity in this study is the predictable target position. In previous studies, the position of the target stimulus was unpredictable, which encouraged participants to rapidly withdraw attention from successfully localized targets back to central fixation. In contrast, the two relevant positions for the line comparison of the present study were predictable. Therefore, attention was probably directed to the task-relevant positions in a sustained manner, which may account for the protraction of the contralateral negativity beyond the N2pc time range. However, alternative accounts are possible. For instance, it is possible that the attentional processes involved in the comparison of two stimuli take longer than processes involved in the identification of a

single stimulus (see Grubert & Eimer, 2016a, Experiment 1, for similar findings). More research is needed to clarify this issue.

General Discussion

We investigated how attention was distributed inside the focus of attention when equally relevant stimuli were differently salient. Observers performed a same-different task on the orientation of lines placed on two non-adjacent locations in the visual field. The lines were surrounded by task-irrelevant geometric shapes. On half of all trials, one of those shapes at the location of one of the target lines was a color or shape singleton. When the two targets were arranged on opposite sides of fixation, we observed a positivity contralateral to the salient singleton in the N2 time range (Experiment 1), suggesting that task-irrelevant singletons were attentionally suppressed (P_D). When one of the targets was on the vertical meridian and the other on a lateral position (Experiment 2), we found solid N2pcs to lateralized line targets during singleton-absent trials. Critically, this N2pc to lateral line targets was abolished when it was surrounded by a salient singleton. We suggest that the elimination of this N2pc is a result of the singleton P_D cancelling out the N2pc to the lateral target line (see Gaspar & McDonald, 2014; Hickey et al., 2009). Further, the N2pc to the lateral element was enhanced when the singleton appeared on a central position as compared to when it was absent, suggesting that excitatory mechanisms can be transiently deployed inside the focus of attention. Overall, our results provide no evidence for attentional capture by the salient singleton, as predicted by theories arguing for bottom-up control of visual attention (Itti & Koch, 2001; Theeuwes, 2010), but favor top-down control mechanisms (suppression of task-irrelevant distractors, see Gaspelin & Luck, 2018).

Conditions favoring suppression

As outlined in the Introduction, there is evidence for both attentional capture and attentional suppression in electrophysiological investigations of visual search in the additional singleton paradigm. We have recently argued that the occurrence of capture or suppression may depend on the difficulty of the search task. In particular, distractor suppression occurred with easy searches, whereas capture by distractors occurred with difficult searches. For instance, salient color distractors capture attention when target and distractors swap roles from trial to trial (Burra & Kerzel, 2013; Hickey et al., 2006; Kiss et al., 2012), which makes the search task difficult and results in large behavioral interference from the distractor (Theeuwes, 1991). In contrast, fixed target and distractor features result only

in small behavioral interference (Theeuwes, 1992) and allow for attentional suppression of the distractor (Burra & Kerzel, 2013; Jannati et al., 2013). Apart from target predictability, the difficulty of the search task may vary as a function of target-nontarget similarity (Duncan & Humphreys, 1989). Low target-nontarget similarity results in easy search and distractor suppression, whereas high target-nontarget similarity results in difficult search and attentional capture by the distractor (Barras & Kerzel, 2017). Similarly, high nontarget-nontarget similarity (i.e., homogeneous backgrounds) results in easy search and attentional suppression of the distractor, whereas low nontarget-nontarget similarity (i.e., heterogeneous backgrounds) results in difficult search and attentional capture (Feldmann-Wüstefeld & Schubö, 2013).

The task in the present study was easy because the relevant target positions were known in advance and the presentation time was unlimited. The relatively short overall RTs of 655 and 765 ms in Experiments 1 and 2, respectively, and the relatively low overall error rates of 6-7% confirm this point. Thus, the low difficulty of the same-different task resembles studies where attentional suppression was observed. In particular, the fact that stimulus positions were predictable may have favored suppression over capture. In a previous study on the relation between saccadic and attentional capture, attentional suppression as indexed by the P_D was more pronounced when the target position was predictable (Experiment 2 in Weaver et al., 2017). Therefore, chances of finding capture rather than suppression of salient stimuli inside a wide focus of attention may increase when the target positions change randomly from trial to trial. We leave this issue to future research. Further, it might be interesting to investigate whether the distribution of attention across two attended locations changes when task difficulty is increased, for instance by masking the target stimuli (e.g., Duncan, Ward, & Shapiro, 1994). It is possible that observers direct their attention to the most salient element under time pressure. However, previous research on the additional singleton paradigm suggests the opposite, namely that attentional capture turns into attentional suppression when the presentation of the search display changed from the typically unlimited viewing time to only 200 ms (Kiss et al., 2012).

Functional considerations

A final consideration concerns the functional benefit of suppressing salient elements inside the focus of attention despite the absence of a task-related incentive to deviate from an equal distribution of attention. In visual search tasks, attentional suppression is believed

to bias attention away from a salient distractor towards the target (e.g., Gaspar & McDonald, 2014). Because the target positions were fixed, there was no need to search for the target position and it is therefore unlikely that suppression helped to locate the target.

In general, the role of attention is to bias the processing of several stimuli that compete for selection in favor of behaviorally relevant stimuli (Desimone & Duncan, 1995; Luck, Girelli, McDermott, & Ford, 1997). A typical example for ambiguity resolution by attention is the visual search paradigm, where several stimuli compete for selection, but participants have to select only one stimulus, the target, for further processing. In the same-different paradigm investigated here, however, the task of attention may be the opposite. Attention may serve to restore balanced processing of two stimuli according to task demands if one stimulus, the singleton, has acquired a competitive advantage because of its saliency. The competitive advantage of the salient stimuli was referred to as "attend-to-me" signal in previous research (Sawaki & Luck, 2010). However, our results from the N1 interval show that the attend-to-me signal cannot be equated with the Ppc component, because the early positivity to salient stimuli was not always observed. In particular, it was observed for both color and shape in Experiment 1, but only for color in Experiment 2. Possibly, both attentional selection and salience computation contribute to the early positivity (Barras & Kerzel, 2017; Weaver et al., 2017). Alternatively, the Ppc may sometimes be missed because of its small magnitude. Nonetheless, it is clear that the same-different task required equal distribution of attention between the two response-relevant locations. We suggest that attentional suppression, as evidenced by the P_D to color and shape singletons in the N2 interval, assured equal consideration of both target locations despite the competitive advantage conferred to the more salient stimulus. In contrast, in visual search, the P_D serves to inhibit salient, but irrelevant stimuli to avoid selection errors (Sawaki et al., 2012; Sawaki & Luck, 2010).

In sum, we investigated how attention is distributed inside the focus of attention. When observers attended to two locations, we found that a salient-but-irrelevant stimulus inside the focus of attention was suppressed. These results are at odds with theories

claiming that attention is controlled by visual salience but may be accommodated by approaches emphasizing the role of task requirements and top-down control.

Footnotes

Footnote 1: Consistent with the literature, we use the N2pc and P_D as an index of attentional selection and suppression, respectively. There is a risk of an unjustified reverse inference (e.g., Poldrack, 2011) in this reasoning. However, the N2pc and P_D components are only observed in narrowly defined paradigms (visual search), resulting in a low base rate of these components in other tasks. Therefore, the reverse inference seems justified.

Footnote 2: It has been suggested that the N2pc is composed of the target-related N_T component and the distractor-related P_D component. However, disentangling the two requires conditions where non-targets are absent on lateral positions (Hickey et al., 2009), which was never the case in the present study.

Footnote 3: In order to check for hemispheric asymmetries, we broke down the difference amplitudes (contra minus ipsilateral) into mean amplitudes for left and right electrodes (PO7 and PO8), separately for left and right stimulus positions. The factors electrode location and stimulus position were then added to the ANOVA reported in the text. The difference in amplitude between contra and ipsilateral electrodes resulted in a significant interaction between electrode location and stimulus position, $F(1, 16) = 40.23$, $p < .001$, $\eta_p^2 = .715$. However, there were no main effects of electrode location or stimulus position to indicate hemispheric asymmetries. Also, neither electrode location nor stimulus position was involved in any interaction beside the four-way interaction, $F(1, 16) = 3.55$, $p = .078$, $\eta_p^2 = .182$, which corresponds to the interaction of interval and singleton feature reported in the text. Similarly, there were no main effects or interactions of electrode location and stimulus position other than those reported in the text for Experiment 2.

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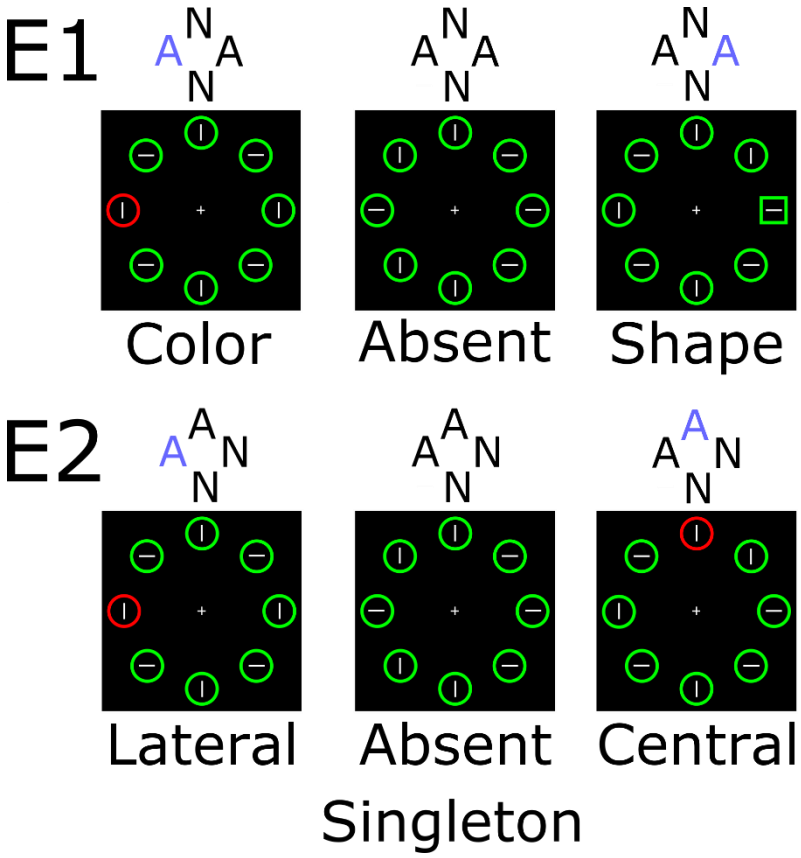

Figure 1. Examples of experimental stimuli in Experiments 1 and 2 (drawn to scale). In Experiment 1, participants had to compare the line orientation to the left and right of fixation (i.e., the 9 and 3 o'clock positions) and respond "same" or "different". The attended positions are indicated by the letter A, whereas nontarget positions are indicated by the letter N. In separate blocks of trials, a color or shape singleton was shown on 50% of trials. The singleton is indicated by a blue letter A. In singleton absent trials, all stimuli were equal in color and shape. In Experiment 2, participants had to compare the line orientations of a lateral (i.e., the 9 or 3 o'clock position) with a central stimulus (i.e., the 12 or 6 o'clock position). The singleton could appear either on the lateral or central position. In the experiments, left/right and top/bottom were equally likely.

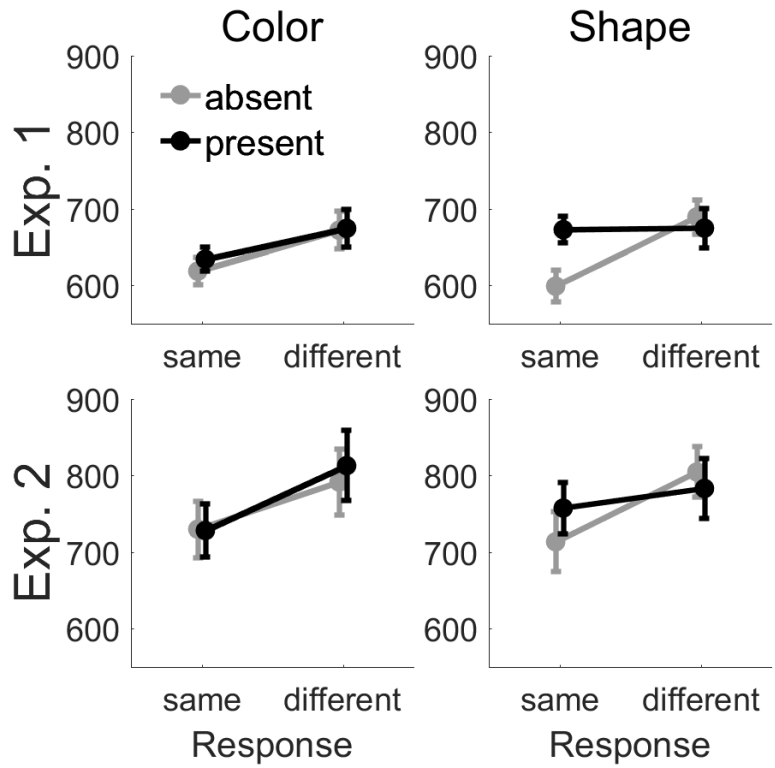

Figure 2. Mean reaction times (in ms, on y-axis) from Experiments 1 and 2 are shown in the upper and lower rows, respectively. Results from blocks with color and shape singletons are shown in the left and right column, respectively. Mean reaction times are shown as a function of singleton presence (absent, present) and response (same, different). Error bars show the between-subject standard error of the mean.

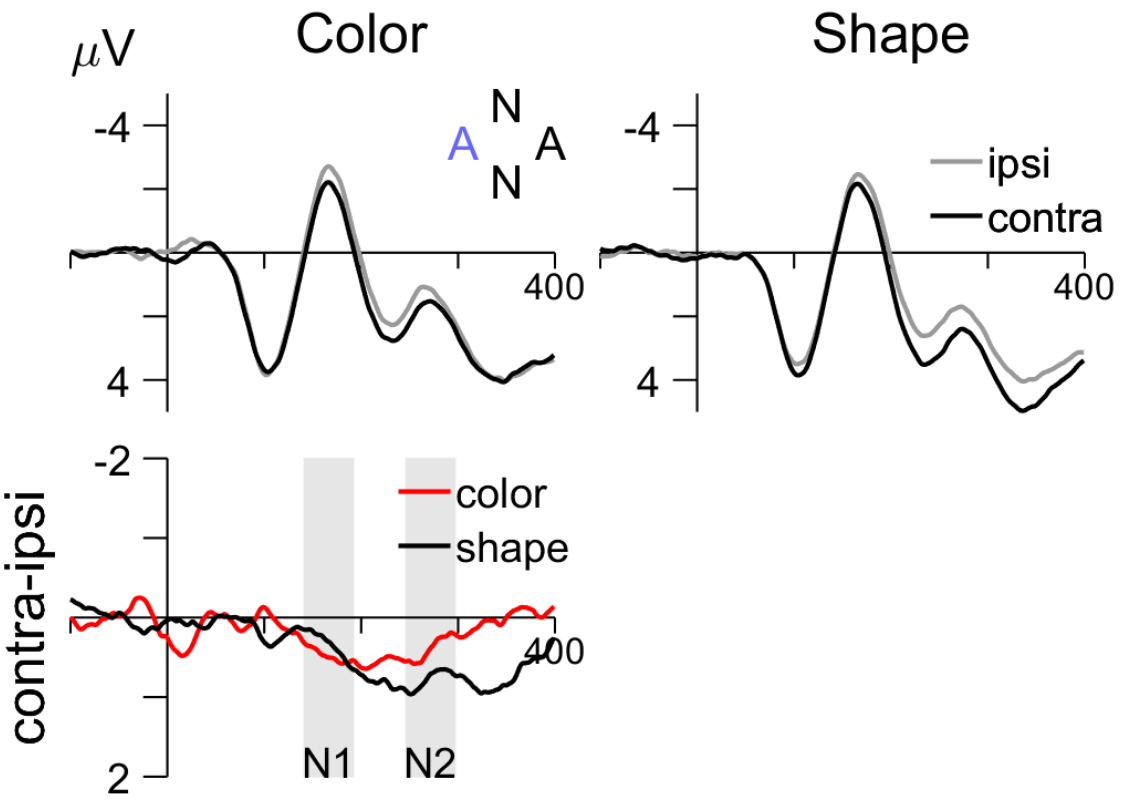

Figure 3. Electrophysiological results from Experiment 1 where line orientations on the horizontal midline were compared. The color or shape singleton appeared on the left or right position. The upper graphs show the event-related potentials at electrodes PO7/8 for ipsi- and contralateral singletons. The lower graph shows the difference waves (contralateral minus ipsilateral) for color and shape singletons. Insets illustrate the position of the attended stimuli (A), the singleton (in blue), and nontargets (N). The gray rectangles show the averaging intervals centered on the peak of the N1 and N2 of the nonlateralized event-related potential.

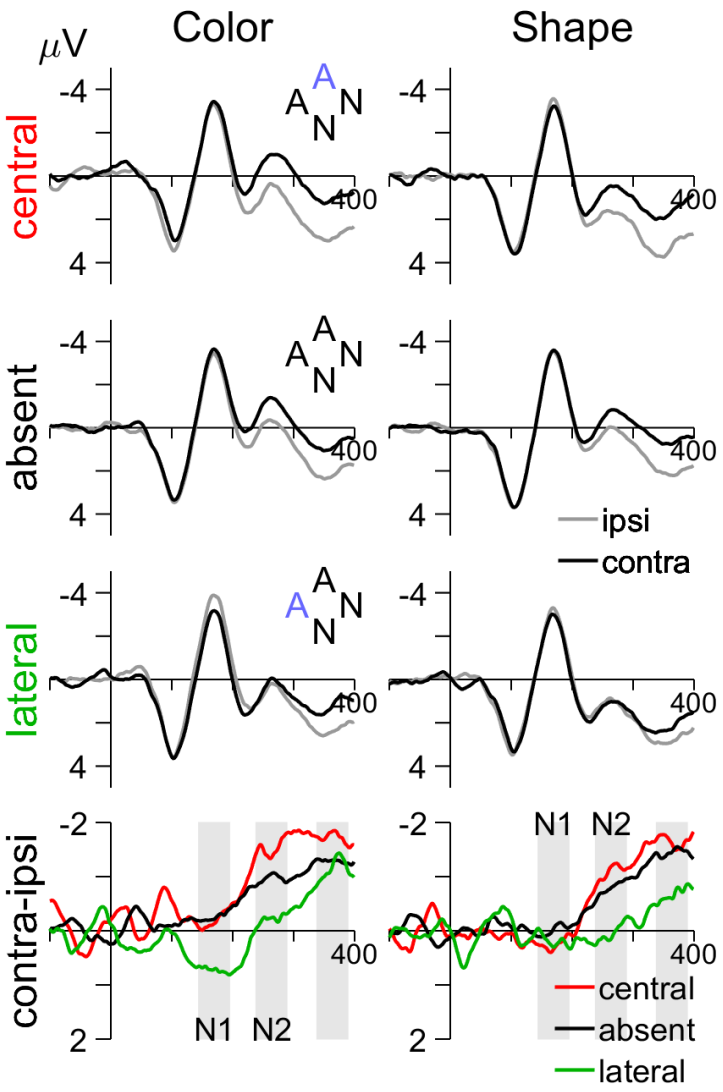

Figure 4. Electrophysiological results from Experiment 2 where participants compared a central and a lateral stimulus. The singleton appeared on the lateral or central position, or it was absent. The first three rows show ipsi- and contralateral waveforms to the lateral element at electrodes PO7/8 when the singleton was on the central position, when it was absent, and when it was on the lateral position. The bottom row shows the difference between contra- and ipsilateral waveforms. The left and right columns show data from blocks with color and shape singleton, respectively. Insets show the schematic position of the attended stimuli (A), the singleton (in blue), and nontargets (N). The gray rectangles

show the averaging windows centered on the peaks of the N1, N2, and on N2+100ms, of the nonlateralized event-related potential.